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CHARACTERISTICS OF SPAWNING NESTS OF COLUMBIA RIVER SALMON

By Clifford J. Burner

FISHERY BULLETIN 61

From Fishery Bulletin of the Fish and Wildlife Service

VOLUME 52

UNITED STATES GOVERNMENT PRINTING OFFICE • WASHINGTON : 1951

For sale by the Superintendent of Documents, U. S. Government Printing Office, Washington 25, D. C.
Price 20 cents

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CHARACTERISTICS OF SPAWNING NESTS OF COLUMBIA RIVER SALMON

By CLIFFORD J. BURNER, *Fishery Research Biologist*

Construction of Grand Coulee Dam across the main stem of the Columbia River raised a serious problem concerning the salmon that spawned in the upper reaches of the river and produced an important part of the west-coast catch. Grand Coulee was to be a high dam, with a tailrace-forebay difference of about 350 feet. Although it was possible to provide reasonably safe passage upstream past the dam for the adult salmon, the cost would be extremely high. Of greater importance was the probability that the salmon fingerlings on their way to the sea would be killed in passing down the spillway or through the turbines. It was decided, therefore, to relocate the salmon runs that spawned above the Grand Coulee site in four tributary systems entering the Columbia River below that site. The Wenatchee, Entiat, Methow, and Okanogan Rivers were selected to receive the transplanted salmon.

One of the many questions in connection with the relocation was how many salmon should be placed in each stream or section of stream to get the maximum yield of spawn and fry. To answer this question, a study was made of the spawning habits of four species of Pacific salmon of the genus *Oncorhynchus*. These are the chinook (*O. tschawytscha*), the silver (*O. kisutch*), the chum (*O. keta*), and the blueback (*O. nerka*). This study was concerned particularly with the type of stream bottom that a given species uses for spawning, and the space occupied by a pair of spawning fish for the nest, or redd. The study included redds of salmon spawning naturally in some of the lower Columbia River tributaries and redds of transplanted spawners in the foster rivers. The information obtained was used in planning and carrying out the maintenance project (Fish and Manavan 1948) but was not published.

At this time, in view of the program for the development of the lower Columbia River tributaries in the interest of salmon production, it seems worth while to set forth the results of the study so that they may be available for reference.

GENERAL LIFE HISTORY

All species of Pacific salmon are anadromous, that is, the adults migrate from the ocean into fresh-water streams to spawn. They proceed up rivers, such as the Columbia, until they arrive at the same tributary where they themselves began life some years before. Very few stray to other streams. The female salmon deposits her eggs in a nest, or redd, which she digs in the gravel of the stream or shallow lake-shore waters. In the process of egg laying, the fertilized ova are covered with successive layers of gravel to a depth of several inches. The time required for the eggs to hatch depends on the temperature of the water. Newly hatched fish live in the gravel of the redd and gradually absorb the food in the abdominal yolk sac. At the end of this period, usually in the late winter or early spring, they struggle up through the gravel and begin to seek food. How long the young fish stay in fresh water varies considerably with the species, but eventually they migrate downstream to the sea, where they remain from 1 to 3 years and grow rapidly. When they approach sexual maturity, they return to fresh water to spawn and thereby complete the cycle. All Pacific salmon die after spawning.

CRITERIA OF A MATURE REDD

At the outset of this study, it was necessary to determine at which stage of development a redd should be measured. Redd building may be divided into three stages, prespawning, spawning, and postspawning. During the prespawning stage, the female salmon is green, that is, the eggs are neither ripe nor loose in the ovaries. Males are seldom in attendance, and are frightened away by the female, who repels all intruders of either sex. The female digs the redd as she turns on either side, at an angle of about 45° to the current, head upstream, body arched, and makes a series of violent flexions with body and tail. (See fig. 1.) The tail strikes the gravel occasionally and the strong-boiling current created carries gravel and

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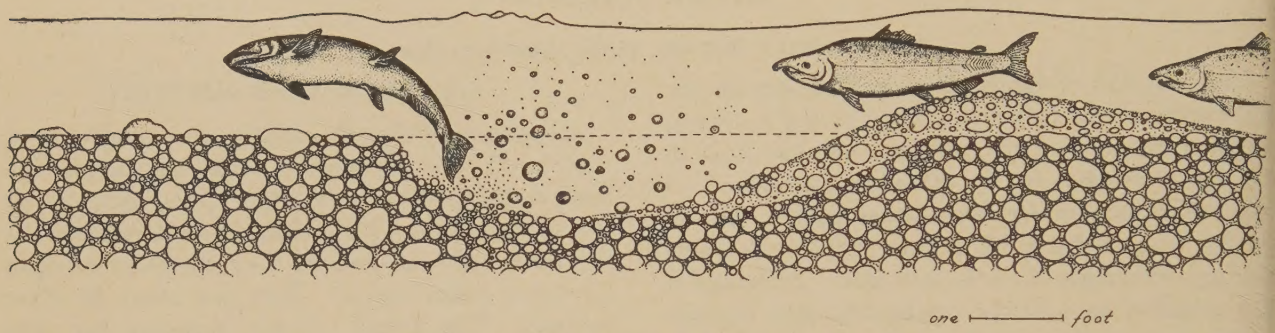


FIGURE 1.—Redd making. Female digging.

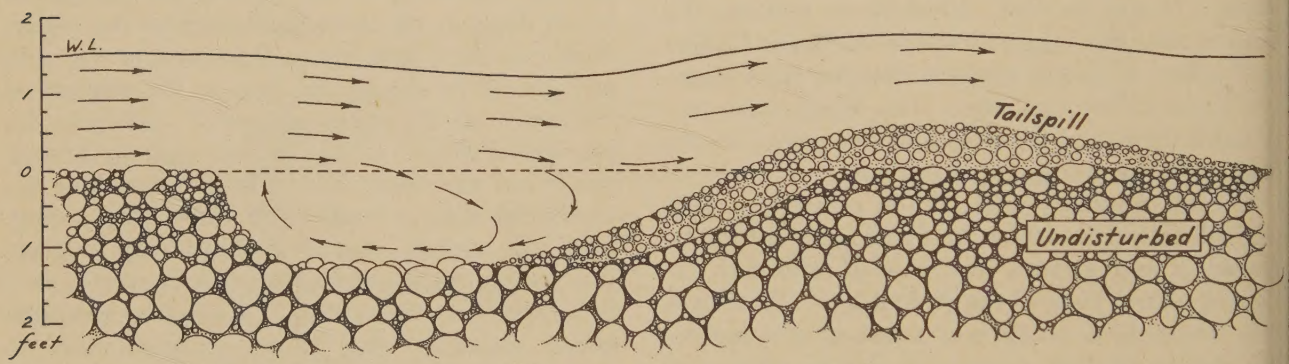


FIGURE 2.—Typical currents in a redd.

silt a short distance downstream. This material spreads out in a flat semicircle at first; then, as the digging upstream proceeds, it collects into a loose pile called the tailspill. With more digging, the redd assumes a long oval shape about twice the length of the salmon and several inches deep. The prespawning digging of the redd may go on for as many as 5 days.

At the beginning of the spawning stage, the nest is ready for the eggs. All loose gravel and fine material have been removed from the pot, or center of the redd, whose shape is such that any current in the bottom flows upstream (see fig. 2), then upward and outward. Usually there remain in the pot large stones too heavy for the fish to move far, and the crevices between these rocks provide excellent lodgment for the eggs. Males are constantly present now. The female alternately digs at the redd and settles back into the depression to release eggs. A male then moves quickly alongside the resting female, as in figure 3, curves his body against hers, and releases sperm in a small milky cloud that settles briefly in the bottom of the redd where the eggs are lodged. The newly deposited eggs are thus surrounded by sperm and eventually fertilized. Excess sperm is carried slightly upstream along the bottom of the redd and gradually carried away by the current. During the spawning stage the redd increases considerably in length and depth, and appears to move upstream as a result of the continued digging at the upstream wall and the filling in of the tailspill area.

The postspawning stage begins after the female

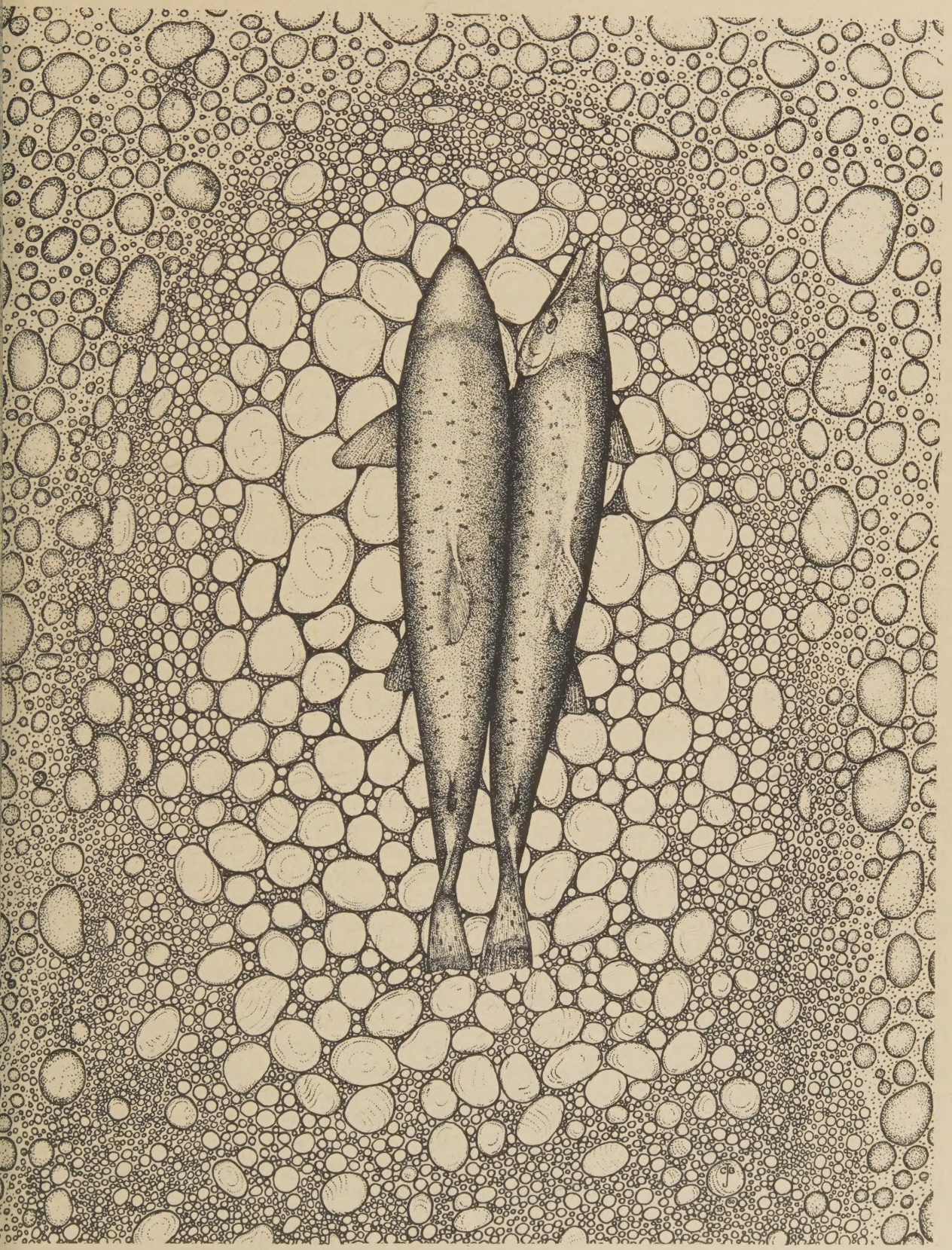


FIGURE 3.—A pair of spawning salmon on a redd.

finishes depositing her eggs. Males are no longer attentive. The female is gaunt and spent, but she continues to dig at the gravel with ever-weakening efforts until she dies. This post-spawning digging, which may continue for 10 days, becomes shallow, off-center, and ineffective. The area of the nest is increased without (after the first day at least) adding to the protection of the eggs.

In view of these facts, a mature redd is considered one in which all egg-laying activities have been concluded, and some postspawning digging has been accomplished.

Several criteria were used to determine whether an observed redd was mature: (1) The gaunt and spent appearance of a lone female salmon still digging—considered the most reliable criterion; (2) the infrequency of the mating act, which becomes sporadic as the supply of eggs is exhausted; and (3) the presence of freshly covered eggs in a redd unoccupied by salmon. Most of the redds measured during the study met the first criterion. For redds observed daily, the second criterion indicated near maturity. Some blueback-salmon redds in which no fish were present were considered mature on the basis of the third criterion.

MEASUREMENTS AND METHODS

Size of the redds was determined by wading into the stream and taking the length, depth, and several width measurements. The outline of the redd was sketched to scale on engineer's notebook paper, with all pronounced irregularities drawn in. Later, in the laboratory, a planimeter was used to compute the area. The entire excavated portion of the redd back to the tailspill's highest point was included in the measurement. The prespawning-digging area, usually located directly under the crown of the tailspill, was thereby included. The long tapering downstream slope of the tailspill was not considered an essential part of the nest measurement, for several reasons: Live eggs were rarely found there; the velocity of the current would carry fine sand and lighter silt considerable distances, resulting in elongation of the slope; and often the downstream slope of the tailspill of one redd would be disrupted by salmon making redds immediately below it. Such tailspill encroachment never proceeded far enough to endanger the eggs laid in the neighboring redd.

Depth measurements were taken from the surface of the water at 1-foot intervals starting at stream bed at the upstream edge of the redd, down the central axis, through the deepest portion, and over the tailspill. A cross section at the greatest depth of the redd was taken in similar fashion from the stream bed on one side to the stream bed on the other.

The gravel composition for each redd was arrived at by estimating the amount of large, medium, and small gravel that had been exposed. The term "large" gravel is used to describe stones more than 6 inches in diameter, but not necessarily round. "Medium" applies to stones from 6 inches down to 3 inches. "Small" applies to those less than 3 inches, but larger than heavy sand.

Stream velocities were taken by clocking a bit of drift over a measured course. The currents and other flow conditions in a redd were determined with an aqueous solution of potassium permanganate.

The times of the salmons' first entry into the streams, the times of first redd digging and of peak of spawning, average stream and redd depths, and water velocities and temperatures are shown in the table.

Except in small, sparsely populated creeks, no attempt was made to measure all the redds in a stream. In rivers thickly covered with redds throughout their length, only representative sections were observed, but all the redds in such sections were measured, in order to avoid selection. In these sections each redd was marked by driving a stake at the downstream slope of the tailspill, or by placing a number on a tree opposite the redd. The stakes facilitated observation, from day to day, of the redd-digging progress of an individual salmon. Figure 4 is a diagram of a redd that was marked on the first day of digging and measured daily thereafter. In this diagram, it will be seen that redd digging extended from September 20 to October 8. The sign of Venus (♀) below the line indicates the female, present each day the redd was measured. The sign of Mars (♂) above the line shows for each day the number of male salmon actively attending and fighting for the privilege of fertilization.

Summary of information gathered on spawning of salmon in selected streams

	Chinook salmon							Silver salmon in Toutle River (1938)	Chum salmon in lower-Columbia tributaries [1] (1938)	Blueback salmon			
	Spring run		Summer run			Fall run							
	Ohanapecosh River (1938)	Nason Creek (1939)	Entiat River (1939)	Wenatchee River (1939)	White River (1939)	Kalama River (1938)	Toutle River (1938)			White River (1939)	Little Wenatchee River (1939)	Wenatchee River (1939)	Okanogan River (1939)
Spawning schedule:													
First entered stream	[2]	[3]	[3]	[3]	[3]	Sept. 9	[2]	[2]	[2]	[3]	[3]	[3]	[3]
First redd digging	Aug. 20	Aug. 21	Sept. 7	Sept. 8	Sept. 23	Sept. 20	Sept. 27	[2]	[2]	Oct. 11	Sept. 17	Oct. 2	[2]
Peak of spawning	Aug. 28	Aug. 31	[4]	Sept. 20	[4]	Sept. 30	[4]	Oct. 22	Nov. 22	Oct. 20	Oct. 12	Oct. 8	[2]
Spawning ended	Sept. 10	Sept. 15	Nov. 15	Oct. 25	Oct. 15	[2]	Nov. 2	[2]	[2]	[3]	Nov. 4	Oct. 31	Nov. 15
Depth of stream: [5]													
Average (mean)—inches	14	8.6	16	13	10	14	11.6	7.8	10	11.5	12	13	9
Minimum—do	2	3	7	4	6	3	3	2	2	3	2	5	4
Maximum—do	36	18	26	30	16	48	24	26	30	37	24	28	17
Depth of redds: [6]													
Average (mean)—do	9	8.5	10	9.7	9.3	10	10.7	8	8.5	5.5	5.7	4.2	5
Minimum—do	3	4	4	4	5	2	4	3	3	3	3	2	2
Maximum—do	20	14	19	18	14	17	18	20	17	9	11	8	9
Velocity of water:													
Average (mean)—cubic feet a second	[2]	2	1.5	2	1.7	2	1.3	[2]	[2]	1.6	1.7	1.8	1.7
Minimum—do	[2]	.5	1	1	1.4	1	1	[2]	[2]	1	1	1.7	1.5
Maximum—do	[2]	3.5	2	3	2	3.5	3	[2]	[2]	1.8	1.9	2	2
Temperature (Fahrenheit) of water:													
Minimum—degrees	51	47	40	55	47	52	42	42	40	44	48	54	47
Maximum—do	53	52	55	62	51	61	58	58	44	49	51	55	48

[1] Germany Creek, Abernethy Creek, Elokomin River, and Grays River.
[2] No data.
[3] Transplanted.
[4] Indefinite.
[5] Average measurements taken from surface to stream bed at each side and at upstream end of each redd.
[6] Depth below stream bed, taken at deepest part of redd.

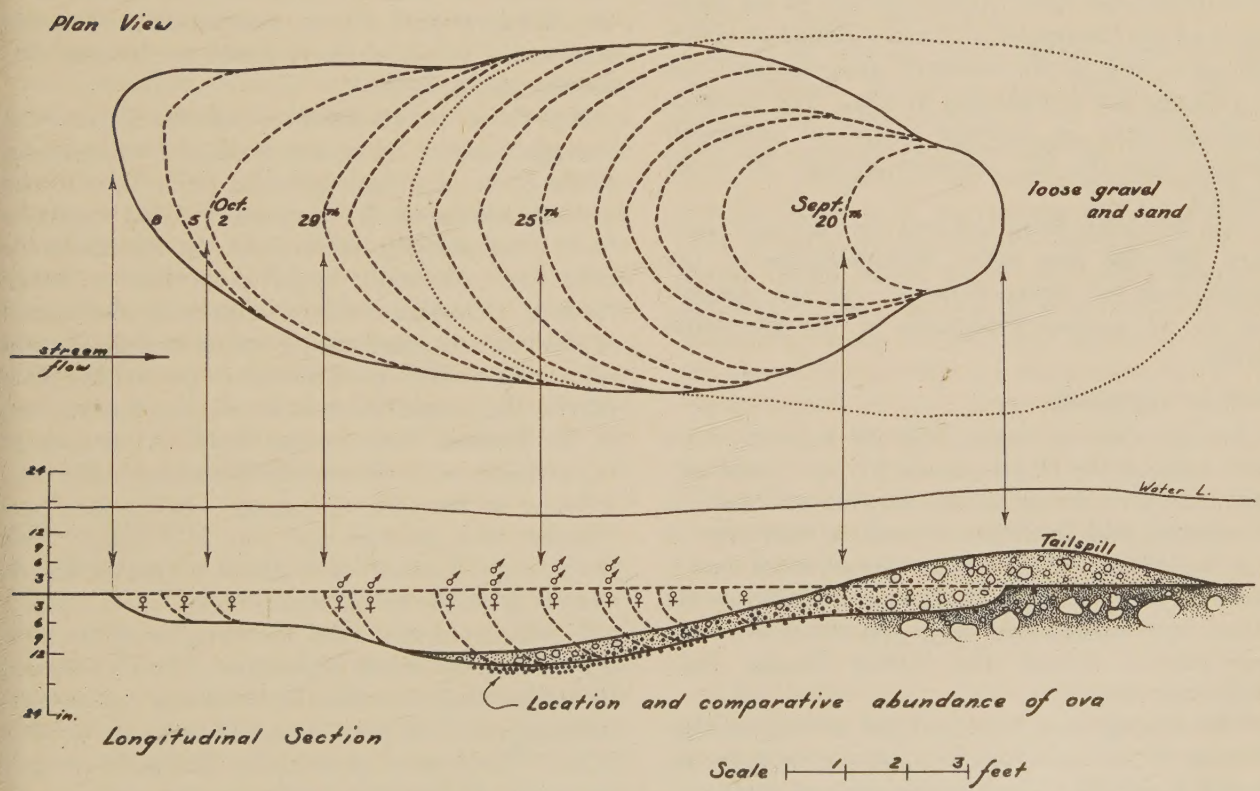


FIGURE 4.—Diagrammatic views of a fall chinook salmon redd measured daily.

CHINOOK SALMON

The chinook salmon is native to the Pacific coast from California to Alaska. Some runs extend from Bering Strait to the southern Siberian coast. By transplantation of fertilized eggs, runs have been established in the St. Lawrence River and in certain parts of New Zealand. The Columbia River supports the largest population of the species.

In the Columbia River, most of the chinook salmon migrate upstream from March through September. The migration is divided into three more or less distinct classes, and the fish are referred to as spring-run, summer-run, and fall-run chinooks, according to the time they leave the ocean and start on their upstream journey. The smaller spring chinooks, which average about 15 pounds in weight, ascend the Columbia River system for considerable distances and spawn in headwaters from mid-July to mid-September. The larger summer chinooks do not go as far upstream as the spring chinooks, and the time of spawning is later, from September to mid-November. The fall chinooks spawn chiefly in the lower Columbia River tributaries and in the main stems of the Columbia and Snake Rivers at about the same time as the summer chinooks, and the two classes are comparable in size. The summer chinooks have an average weight of about 30 pounds, and the fall chinooks average 20 to 25 pounds.

The following three sections describe and compare the size and other characteristics of the redds made by spring, summer, and fall chinook salmon, in several tributaries of the Columbia River.

SPRING CHINOOK

Investigation of spring chinook salmon redds was made in the Ohanapecosh River, a tributary of the Cowlitz River (which is a lower-Columbia tributary), and in Nason Creek, a tributary of the Wenatchee River. The Ohanapecosh has a natural run of spring chinook salmon, whereas the Nason was one of the streams into which fish were transplanted during the Grand Coulee fish-maintenance project.

The average redd size and gravel composition of these two streams may be compared in figure 5*a*, circles A and B. The Ohanapecosh, a mountain stream, contained a high proportion of large rubble about the size of a football. Because of the large-gravel component, the Ohanapecosh redds were considerably smaller (2.9 square yards) than Nason Creek redds (4.9 square yards). The Ohanapecosh redds contained an average of 59 percent medium and small gravel, whereas the Nason Creek redds averaged 86 percent medium and small.

Spawning times, stream depths at the redds, depths of redds, and water velocities and temperatures for the spring-chinook redds in the two streams are given in the table.

SUMMER CHINOOK

The spawning of summer chinook salmon was studied in the Entiat River, the Wenatchee River, and the White River tributary of Wenatchee Lake. These are streams selected as foster rivers for some thousands of the chinook salmon blocked by Grand Coulee Dam. The spawning redds measured were made by the transplanted salmon, trapped at Rock Island Dam near Wenatchee, Wash., in July, August, September, and October. Because of the similarity of summer-run to fall-run chinook salmon in all but time of migration, I have combined the measurements of the summer-chinook redds with those of fall-chinook redds in the size frequency graph, figure 7.

For the 41 redds measured in the Entiat, the average size was 7.8 square yards. A comparison of the Entiat average, figure 5*a*, circle C, with the average nest areas for summer and fall chinooks from other streams shows that the Entiat River redds were distinctly larger than those in other streams. The Entiat River contains an abundance of medium and small rubble which facilitated redd construction and resulted in large redds. The degree of cementation was less in the Entiat than in the Kalama River or the Toutle River (where fall-chinook redds were studied) and probably contributed to the ease of digging. Subsurface percolation was greater, and this is a factor that governs the location of redds to a greater extent than is generally recognized.

It was noted that most spawning took place on gravel through which there was a flow of water. The flow was detected by releasing potassium-permanganate solution in test holes in the stream beds. There were areas in the Entiat River and in nearly all streams examined, apparently unexcelled for redd building and where trial redds were

ible, that were deserted by salmon for no other ertainable reason than that there was little or flow of water through the gravel. Gravel nly cemented with silt and clay binders usually ked a percolating flow and was avoided by tiat River chinooks and by salmon in other eams. All species showed a decided preference moderately bound stream-bed materials in ce of either loose shingle (free-rolling gravel) or mly bound rubble.

Nearly all spawning of summer chinook salmon the White River took place in areas of the stream at contained 95 percent medium and small avel. As shown in figure 5*a*, circle D, 9 redds ere measured and the average nest area was 4.7 uare yards. Although this appears to contradict e inverse-ratio relation between gravel size and dd area, it is not considered significant, in view the small number of redds measured. As its me implies, the White River is clouded by quanties of chalky glacial material during the summer d fall run-off, and this made observations difficult.

The redds studied in the Entiat, Wenatchee, and hite Rivers were made by salmon transplanted each spawning area over a long period of time. location was spaced out in order to keep the xes evenly distributed in each area. As a result, ere was a mixture of stocks, or races, of summer inook on the same spawning areas, and a wide sortment of sizes of redds resulted. Although the mmer chinook are a little larger, as a class, than e fall chinook, their redds contained about the me proportion of large, medium, and small avel as fall-chinook redds. Figure 5*a*, circle E, ows that average redd size and gravel composiin, for summer chinook in the Wenatchee River e comparable to the redd sizes and gravel comsitions for fall chinook in the Toutle River system, figure 5*a*, circles G and H.

ALL CHINOOK

The Kalama River, the Toutle River, and the reen River tributary of the Toutle, were selected r study of fall chinook salmon redds. The outle River is a tributary of the lower Columbia rough the Cowlitz River; the Cowlitz and the alama enter the Columbia only a few miles art, about 60 miles from the sea. Thus, they e neighboring streams and they have somewhat milar watersheds—both are moderately forested and have fair gradients—but here the resemblance ends. Because of an insurmountable falls, the Kalama River has only 7 miles of available spawning area, containing a high proportion of large gravel. Most of the stream bed is of stratified gravel, that is, stream-bed disturbances and subsequent flooding have overlaid the large gravel with successive layers of smaller stones. During redd digging the salmon encountered the substratum of large rocks with the result that the redds resemble oversize underwater Easter egg baskets. The Kalama River fall-chinook redds contained a higher proportion of large gravel than did other fall-chinook redds. (See fig. 5*a*, circle F.)

The Toutle River and its Green River tributary are both accessible through virtually all their lengths, presenting 40 miles or more of stream bed with a greater choice of spawning rubble than is available to the Kalama River fall chinooks. The areas used contained gravel of relatively uniform size with little or no stratification. Whereas the Kalama River redds averaged 5.7 square yards with 41 percent large gravel, the Toutle River redds averaged 6.5 square yards with 11 percent large gravel.

It would appear, from examination of figure 5*a*, circles F, G, and H, and figure 6, that the abundance of large gravel in the Kalama had the effect of reducing the size of the fall-chinook redds there as compared with fall-chinook redds in the Toutle River and its Green River tributary. The slightly smaller average for the size of the Green River redds, figure 5*a*, circle G, may be attributable to the fact that fewer redds were measured; figure 6 shows that the modal size of the Green River redds is greater than that of the Kalama River redds. These differences might be explained on the basis of the mechanics of redd building: the large gravel in the Kalama was difficult to dislodge and to move, so the resulting redds were smaller, whereas the medium gravel of the Toutle River was easier to dig in and produced larger redds.

SILVER SALMON

Silver salmon are distributed throughout the North Pacific from mid-California to Alaska and in Asiatic waters as far south as Japan. The greatest runs are found in the streams of Oregon, Washington, British Columbia, and southeastern

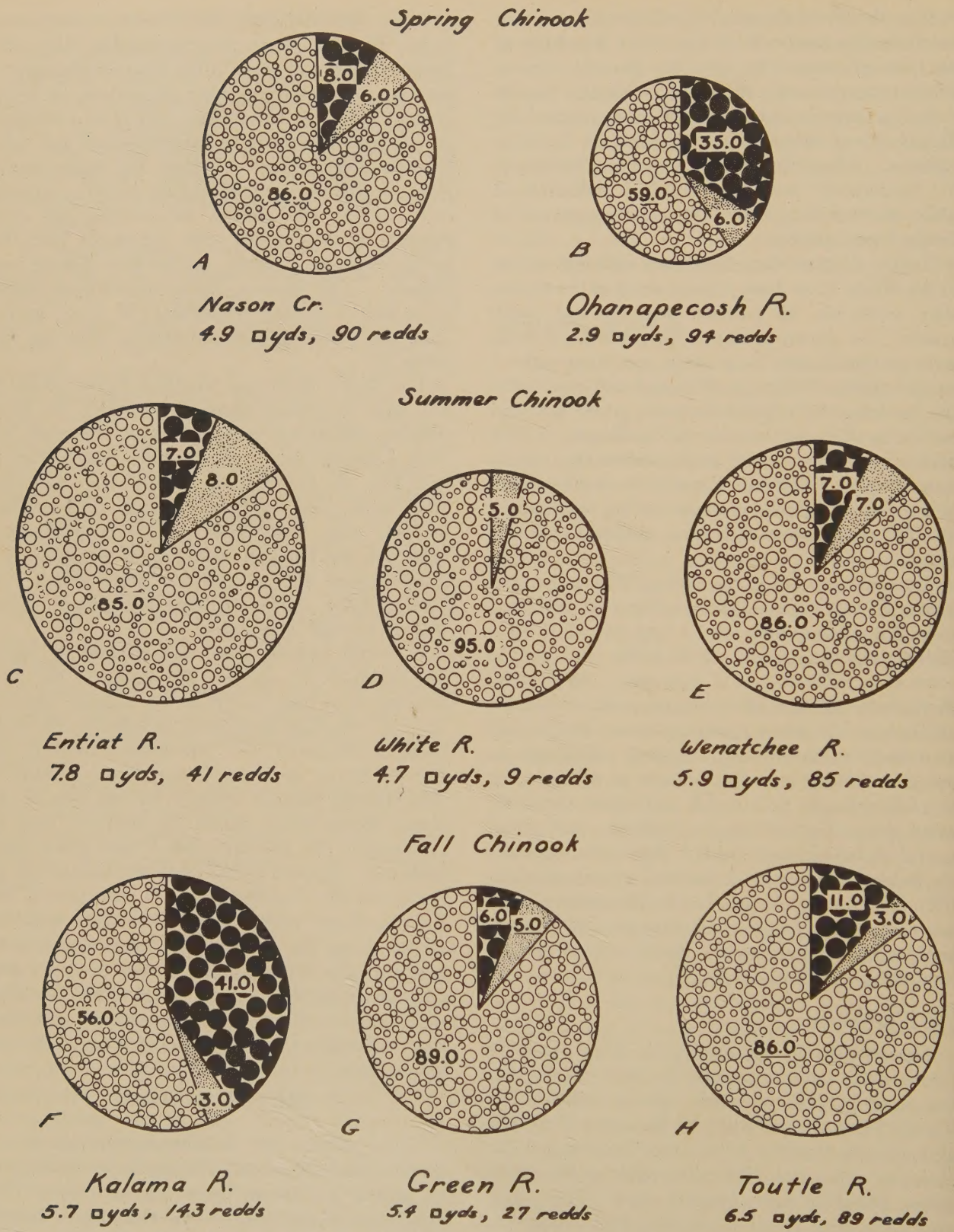
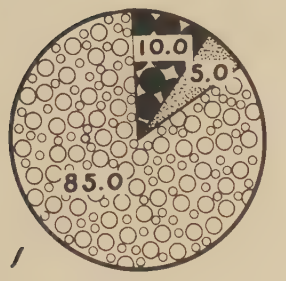


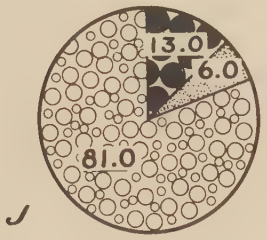
FIGURE 5*a*.—Average size and gravel composition of Columbia River salmon redds.

Silver



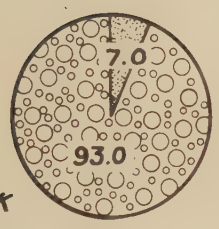
Toutle R.
3.4 □yds, 65 redds

Chum



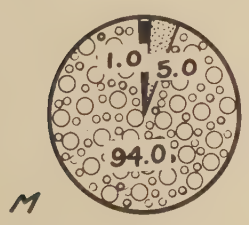
Lower Columbia tribs.
2.7 □yds, 66 redds

Blueback

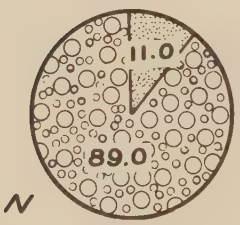


White R.
2.0 □yds, 31 redds

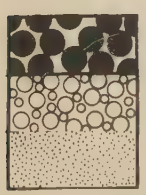
Okanogan R.
2.1 □yds, 37 redds



Wenatchee R.
1.8 □yds, 31 redds



Little Wenatchee R.
2.4 □yds, 42 redds



Large gravel - more than 6" diam.
Medium and Small - 6" or less
Mud - Silt - Sand

FIGURE 5b.—Average size and gravel composition of Columbia River salmon redds.

Alaska. At maturity they average about 9½ pounds in weight and about 24 inches in length.

In the upper Toutle and Green River tributaries of the Columbia, the silver salmon occupied many of the same spawning areas as the fall chinooks, and the two species were found spawning at the same time.

In general, the silver salmon apparently prefered small streams flowing only 3 or 4 cubic feet a second and were present in a number of localities not occupied by the chinook salmon. A comparison of the nesting habits of the two species was obtained at a point where the Toutle River is divided by a large bar into a broad and a narrow channel. The small, 3-foot-wide watercourse was populated exclusively by silver salmon. The wider run, nearly 60 feet across, contained only fall-chinook salmon. In the shallower upper reaches of the Green River tributary, the two species spawned virtually side by side.

The silver salmon demonstrated a redd-building versatility that was not equalled by other species. In the small Beaver Creek tributary of the Green River, a stream of less than 2 cubic feet a second, the bottom was composed of flat chunks of slate-shale rubble that defied classification by the usual gravel standards. The silvers were paired off and spawning in stream-width redds that were end to end for a distance of nearly 2 miles. In the Toutle River, immediately below Spirit Lake, silver-salmon redds assumed bizarre shapes, both in surface outline and in bottom contour, as the fish dug around embedded boulders and fallen trees. This was the only salmon of the four species whose redds contained up to 10 percent mud. The gravel composition of silver-salmon redds is shown in figure 5*b* and the size frequency of the redds is shown in figure 7.

CHUM SALMON

Chum salmon are found in rivers of the Pacific coast from Oregon to the Arctic Ocean and in streams of the northern Japanese islands. In the Columbia River these salmon spawn mainly in the small tributaries only a short distance from the sea. They average 26 inches in length and weigh about 10 pounds at maturity.

The streams selected for a study of chum-salmon spawning, Germany Creek, Abernethy Creek, Elokomin River, and Grays River, are tributaries of the lower Columbia River and only a few miles apart. The chum salmon did not migrate far upstream, and in Abernethy Creek some spawned in tidal water so that the redds were uncovered and dry at the surface during a part of each day. Several of the redds were examined when exposed, and live ova were found in the damp gravel of the nest. At high water, these redds were occupied by spawners, but it was not determined whether they were the original occupants.

Chum salmon were also found spawning in water just deep enough to cover the lateral line of the fish. When disturbed they would dash out of the water onto the banks and flop back into the stream. In thickly populated sections, the redds were ill-defined and overlapped from end to end and laterally. The riffles contained hundreds of opaque dead eggs and a few lives ones. Because of the abundance of spawners and the overlapping of nests, it was necessary to select redds for study on the basis of their individuality of outline and apparent maturity. These salmon were more easily frightened than the other species so that it was difficult to determine whether the females were in continuous possession of their redds. In a few instances it was definitely determined that the same females occupied their nests for at least 3 days.

Of 66 chum-salmon redds measured, the average size was 2.7 square yards (fig. 5*b*, circle J). The proportions of large, medium, and small gravel were similar to the proportions for most of the other species. Chum salmon, even more than other species, avoided firmly cemented gravel bottom and spawned in sections of moderately bound rubble where subgravel flow or percolation was evident.

BLUEBACK SALMON

Blueback salmon is the name applied to the species *O. nerka* within the Columbia River System and a few neighboring streams. In Puget Sound and British Columbia they are called sockeye, and in Alaska, red salmon. In the Columbia River, blueback salmon average 3 pounds in weight and 20 inches in length.

The blueback salmon differs from all the other species in that the spawning redds, with few exceptions, are made only in streams tributary to lakes or along lake shores. The young salmon, on emerging from the gravel of the nest, descend

without delay to the lake and live there at least a year before migrating seaward.

Blueback-salmon redds are perfect models of the nests made by larger salmon of other species. The extent of the redd and the size of the gravel chosen are scaled down to the size of the blueback. The number of redds measured, the average size, and the gravel composition are shown in figure 5*b*, circles K, L, M, and N. The gravel composition was 90 percent or more of medium and small size, with the small gravel (about the size of a golf ball) predominating. The stream-type blueback redd contained a small pot of larger stones to receive the eggs, had a loose tailspill, and was oval. The lake-type redd in the shallows near shore in Osoyoos Lake (Okanogan River watershed) was larger and of irregular shape; because there was no current, the female would dig all around the edge of the nest. As there were relatively few of the lake-type redds, none were measured.

REDD SIZE AND INTERREDD SPACE

In general, for all species of salmon the size of the redds varies in direct proportion to the size of the salmon comprising the run, and in inverse proportion to the size and cementation of the gravel in the stream. The redds made in slow water are larger and more circular in outline, but as a rule are not as deep as those made in rapid water where the hydraulic force helps move the gravel.

On crowded spawning gravels of riffles and rapid runs, some chinook redds overlapped slightly end-to-end because the long tailspill of one redd would be disturbed by the female working directly downstream from it. Only a few redds overlapped laterally. As a matter of fact, few redds of any species were made exactly side by side, but occasionally the redds would form diagonal rows across the streams. For the most part, the female chinook salmon was vigorously averse to the presence of another female immediately upstream from her nest, or one digging directly at the side of her nest, until her own redd was well under way.

The natural tendency of the female salmon to guard the privacy of the redd area made for fairly regular spacing. The more or less symmetrical oval shape of most nests was an additional space factor. The salmon redds in a crowded stream area do not fit into each other like the parts of a jigsaw puzzle, but have spaces between them nearly as great as, or greater than, the areas of the nests themselves. This interredd space varies with the species and also with such physical factors as population pressure, composition and gradient of stream bottom, and water velocity. The ratio of interredd space to redd size appeared to be less for chum salmon and silver salmon than for the other species studied. The contiguous and in some cases superimposed construction of chum-salmon redds may have been the result of overpopulation of the limited spawning areas available in the streams examined. Population pressure noticeably decreased the interredd space of silver salmon in Beaver Creek at the upper limit of spawning, where the stream was wide enough for only one or two redds.

In the Kalama River, the large rubble made for smaller redds, but interredd spacing was about the same as elsewhere—presumably because the nest radius to be defended remained the same for chinook salmon of a given size. In quiet-water areas, both redd size and interredd spacing were proportionately greater than the redd size and interredd spacing in stretches of rapid water where the stream bed had considerable gradient. In rapid water, the spawning salmon were busier with redd digging, so that fewer "dog-fights" occurred. Their distribution on the spawning gravels was more or less uniform, resembling the typical spawning-stream population of moderate riffles.

In general it was noted for chinook salmon that, wherever sufficient spawners were present to utilize virtually all the usable gravel, the interredd space amounted to nearly three times the area occupied by the redds. Thus, the total average area necessary for a pair of spawning fish was about four times the area of the average redd. For other species, the space factor was somewhat less than that for chinook salmon. It is believed, however, that to arrive at a conservative figure for the number of pairs of salmon that can satisfactorily utilize a given area of gravel suitable for spawning, the area should be divided by four times the average size of the redds. Thus, a pair of spawning summer or fall chinook salmon would require approximately 24 square yards of suitable gravel; spring chinook salmon, 16 square yards; silver salmon, 14 square yards; chum

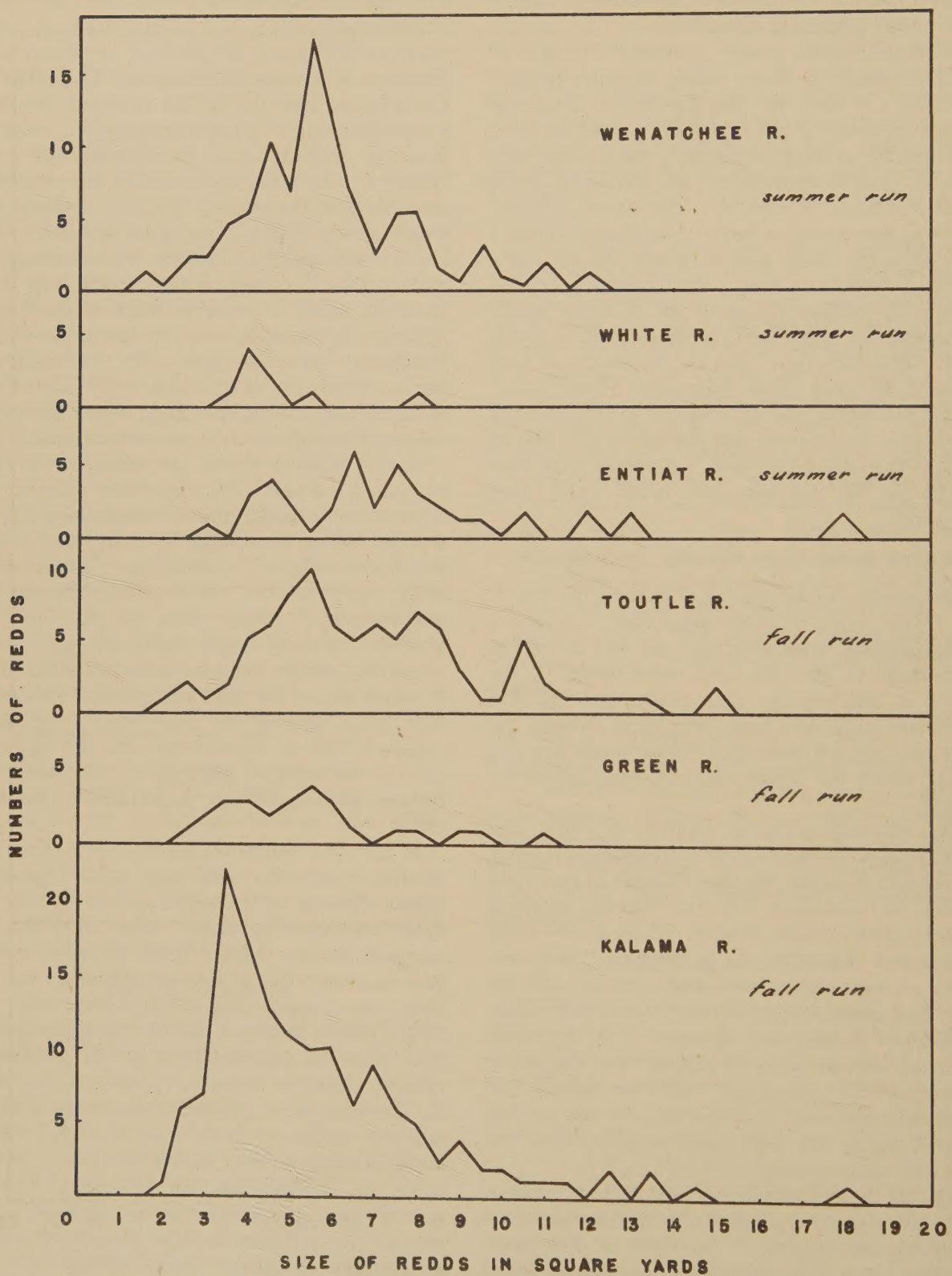

WENATCHEE R.
summer run
WHITE R. summer run
ENTIAT R. summer run
TOUTLE R.
fall run
GREEN R.
fall run
KALAMA R.
fall run
NUMBERS OF REDDS
SIZE OF REDDS IN SQUARE YARDS
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20

FIGURE 6.—Size frequency distribution of summer and fall chinook redds.

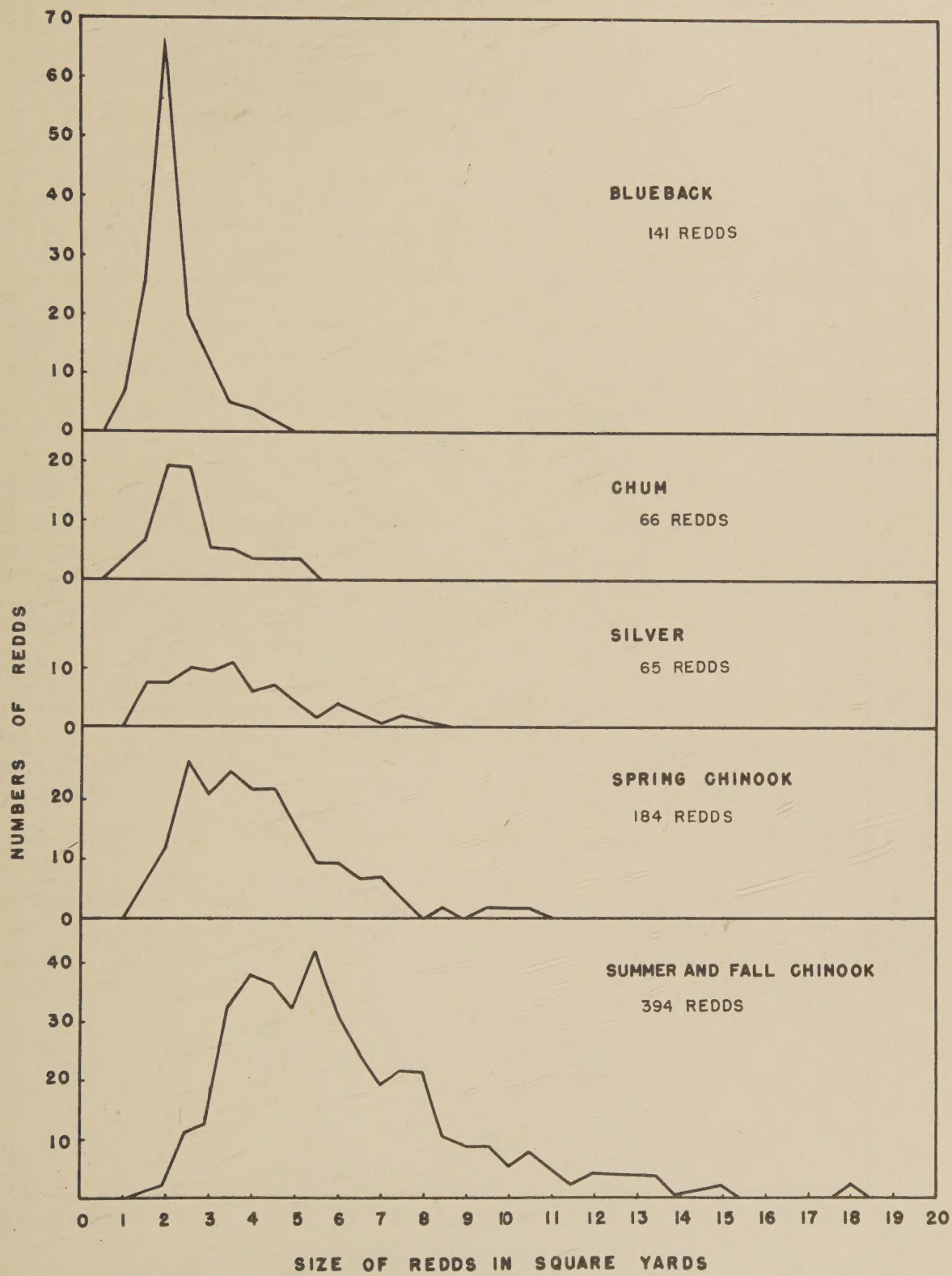


FIGURE 7.—Size frequency distribution of salmon redds from all streams combined.

salmon, 11 square yards; and blueback salmon, 8 square yards.

SUMMARY

1. Observations were made on a large number of chinook, silver, chum, and blueback salmon redds in the Columbia River watershed, and 850 redds were measured.

2. Normally, the female salmon constructs the redd, the male taking no part in this activity.

3. The redd is formed or excavated by the female turning on her side and making violent flexions of the body and tail. The boiling currents set up by this action disturb the gravel of the stream bed which is carried a short distance downstream to form the tailspill.

4. A typical redd is an excavation in the stream bottom, oval in shape, the greatest diameter being lengthwise with the current, and with a tailspill at the downstream end. The center of the redd is referred to as the pot, and it is here that the bulk of the eggs is deposited.

5. Current velocities at spawning areas varied from less than 1 foot a second to 3.5 feet a second. Redds made in fast water were invariably long and narrow; those in quiet water had a broad oval shape.

6. The current in the pot of the redd flows slightly upstream, which favors safe deposition of the eggs in the gravel and is conducive to complete fertilization by the milt of the male salmon.

7. As the spawning progresses, the redd in a sense moves upstream by continued excavation of the upstream edge and filling in of the tailspill area.

8. In general, salmon chose areas of stream bed composed of gravel less than 6 inches in greatest diameter, with the size of the redd inversely proportioned to the size of gravel. Firmly cemented gravel was avoided, though where there was some cementation, the size of the redd was inversely proportioned to the amount of cementation.

9. Percolation of water through the gravel appears to be a requisite of the redd site.

10. In general, salmon prefer areas of stream bottom relatively free of mud or silt for redd-making purposes. Silvers (*O. kisutch*) were the only salmon of the four species which constructed redds in areas of stream bottom containing up to 10 percent mud.

11. Average redd size for the various salmon is as follows: Summer and fall chinook, 6.1 square yards; spring chinook, 3.9 square yards; silver, 3.4 square yards; chum, 2.7 square yards, and blueback, 2.1 square yards.

12. Few redds of any species were made side by side. For the most part, nests were either up or down stream from each other so that they would form diagonal rows across the stream.

13. The tendency of female salmon to prevent other females from getting too close resulted in interredd space approximately three times the size of the redd.

14. By dividing the area suitable for spawning in a given stream by four times the average redd area, a conservative estimate will be obtained of the number of salmon that may satisfactorily spawn in the stream.

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